

# COMPARATIVE OSTEOLOGY OF THE PELVIC GIRDLE OF AUSTRALIAN FROGS AND DESCRIPTION OF A NEW FOSSIL GENUS

by M. J. TYLER\*

## Summary

TYLER, M. J. (1976).—Comparative osteology of the pelvic girdle of Australian frogs and description of a new fossil genus. *Trans. R. Soc. S. Aust.* **100**(1), 3-14, 28 February, 1976.

The osteological characteristics of the pelvic girdle of twenty-five extant genera of Australian frogs of the families Hylidae, Leptodactylidae, Microhylidae and Ranidae are defined. The new Tertiary fossil genus and species *Australobatrachus ilius* are described from the Fladonna Formation. The fossil exhibits a unique lateral ilial groove and is referred tentatively to the family Hylidae.

## Introduction

Of all bones of the anuran skeleton, the ilium has been shown to vary considerably and consistently between families, genera and even species. Iliac are commonly well preserved amongst disarticulated skeletal material, and their features are sufficiently diagnostic to permit identification; for this reason ilia have provided the basis for the recognition of genera and erection of new fossil species (Lynch 1963; Chantell 1964; Holman 1965).

Data on extant species so essential for identification and general comparative purposes are frequently limited, and in the case of Australian frogs, data are particularly deficient. Lynch (1971) provides the only comparative contribution. Confining his interest to leptodactylids, Lynch described the ilia of representatives of nine genera. Since then a fossil ilium of a previously undescribed genus has been reported from the Australian Tertiary by Tyler (1974), and it has proved necessary to examine and describe representative ilia of all of the known living genera in order to describe the new genus and species.

## Material and methods

The dry specimens of the modern species studied were dissected from representatives of 4 families, 25 genera and 60 species, including all genera known in Australia. This material is in the author's collection. The fossil described

herein is in the Palaeontology collection of the South Australian Museum.

With only minor variation, the descriptive terminology used follows Lynch (1971), and the features recognised are shown in Figure 1. Morphometric data were obtained with dial callipers or an eyepiece micrometer. The length of the animals from snout to vent was measured before dissection. Subsequently, the distances between the tip of the dorsal acetabular expansion and the end of the ilial shaft and the span between the anterior margin of the dorsal prominence and the ventral acetabular expansion were measured. The bone measurements were examined to establish relationships between ilial size or proportions and the size of the donor frog.

## Features of the Anuran pelvis

### (A) Pubis

The pubis is customarily a small, roughly triangular, cartilaginous wedge of tissue separating and underlying the ventral borders of the ischium and ilium (Fig. 1). In particularly large species (rarely in small ones), where there is a more intimate degree of fusion of the pelvic components, the pubis is often calcified or ossified.

### (B) Ischium

The ischium is a bony or cartilaginous disc anteriorly fusing with the ilium to provide the posterior half of the acetabulum, and pos-

\* South Australian Museum, North Terrace, Adelaide, S. Aust. 5000. (Present address: Department of Zoology, University of Adelaide, Adelaide, S. Aust. 5000).

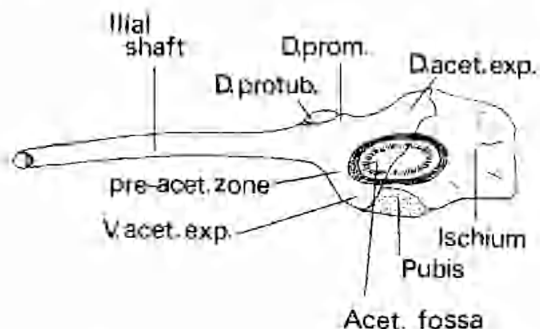


Fig. 1. Left lateral aspect of anuran pelvic girdle. *Abbreviations:* Acet. fossa—acetabular fossa; D. acet. exp.—dorsal acetabular expansion; D. prom.—dorsal prominence; D. protub.—dorsal protuberance; pre-acet. zone—pre-acetabular zone; V. acet. exp.—ventral acetabular expansion.

teriorly forming a plate occupied by numerous muscles communicating with the femur.

The shape of the ischium varies considerably at a specific level and is associated with differences in habits. For example, the development of a particularly large plate posterior to the acetabular fossa is found only in round species with exceptionally short and muscular hind limbs. Similarly, the development of a high, dorsally projecting extension is characteristic of large but agile frogs with powerful hindlimbs. Viewed with the femur as the reference point it is clear that a major shift in the muscle mass can only be brought about by concurrent changes in the development of the ischium.

### (C) Ilium

The ilium is the largest pelvic bone, and consists of an elongate shaft terminating in an axe-head shaped body. It is a paired structure articulating anteriorly with the ventral surface of the sacral diapophysis and posteriorly abutting the ischium and pubis. Various areas of the ilium are recognisable as distinct components:

(a) *Iliac shaft:* The iliac shaft is an elongate and usually slightly curved structure varying from a cylindrical section through vertically oval to more elaborate forms in which there are grooves on the lateral or medial surfaces.

(b) *Dorsal crest:* A smooth bordered crest, rising high as a thin blade, occurs in numerous species of frogs, but is rare amongst Australian forms. It usually arises from the dorsolateral surface of the shaft, and reaches its maximum height within the anterior one-third of the shaft (Fig. 4L).

(c) *Dorsal prominence:* The dorsal prominence is a differentiated area rising on the superior margin of the shaft in a position above or slightly anterior to the acetabulum. It is not present in all species and is scarcely detectable in many others (e.g. in those exhibiting a dorsal crest).

(d) *Dorsal protuberance:* From the body of the dorsal prominence the dorsal protuberance arises as an elongate, rounded or pointed knob. To it attaches the *Musculus gluteus maximus*.

(e) *Dorsal acetabular expansion:* The body of the ilium extends dorsally into a triangular portion of bone superior and posterior to the acetabulum. This projection is termed the dorsal acetabular expansion. It may rise steeply and so meet the ischium in a vertical plane, whilst the anterior face can be at an acute or obtuse angle to the iliac shaft.

(f) *Acetabulum:* Variation in the acetabulum consists of differences in size (relative to adjacent structures), in position in relation to the iliac shaft, and in the width and extent of development of the acetabular rim.

(g) *Ventral acetabular expansion:* The superior segment of the ventral acetabular expansion has been termed the preacetabular zone by Lynch (1971). The considerable variation in this portion of the pelvis is difficult to express, because of the instability of potential reference points such as the acetabulum. Nevertheless, the basic shapes range from the form of a straight line extending ventrally and posteriorly (Fig. 2A, D), a gradual concavity (Fig. 2B), or a concavity of the preacetabular zone and a convexity beneath (Figure 2C).

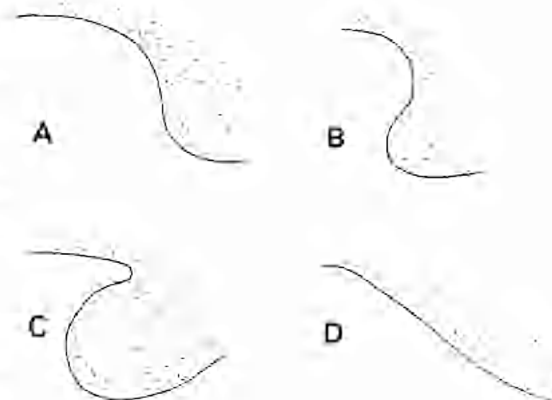


Fig. 2. Variation in the shape of the ventral acetabular expansion viewed from left aspect. See text for explanation.

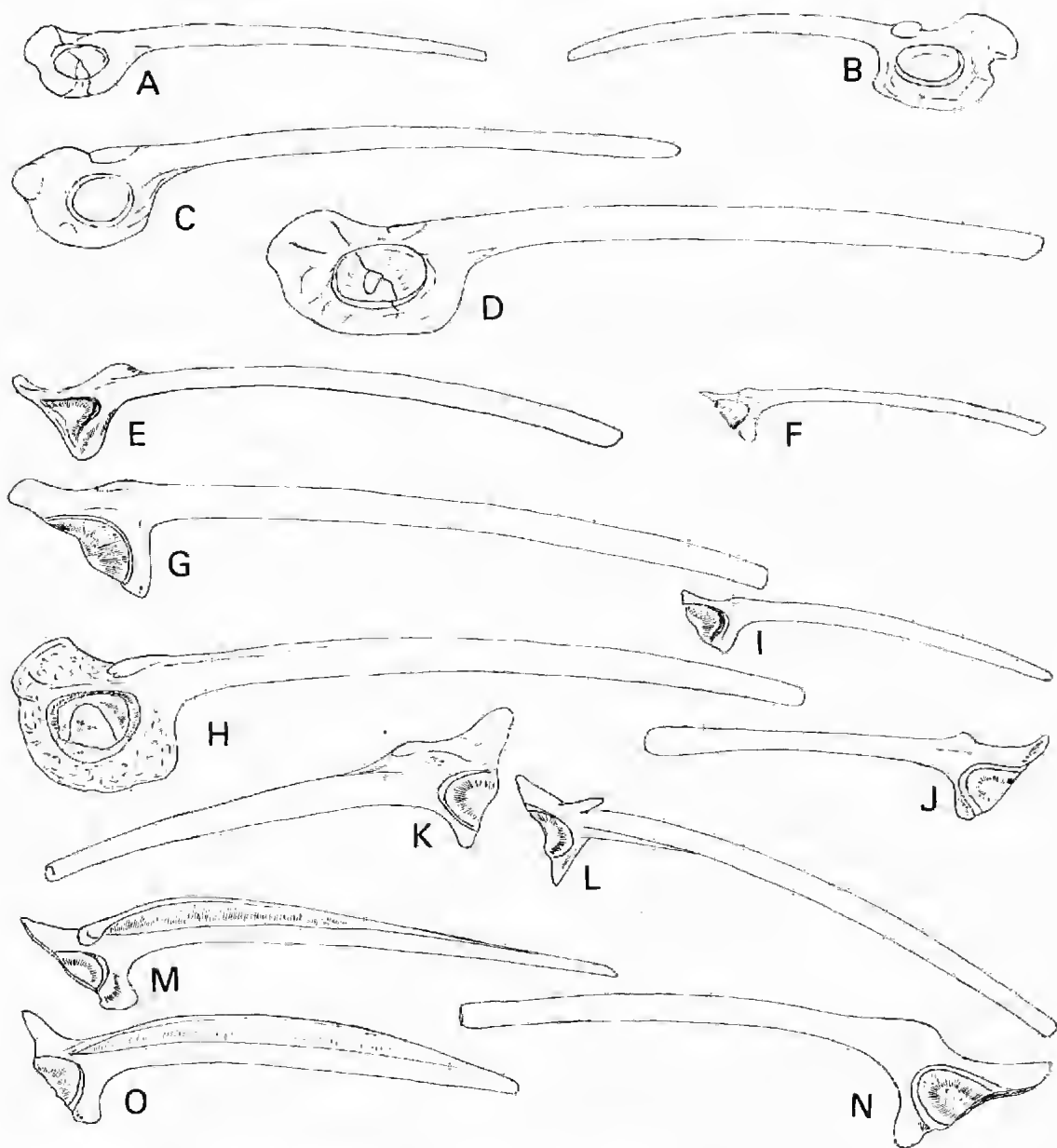


Fig. 3. Pelvis or isolated ilium of hylid and leptodactylid frogs:

- A. *Litoria caerulea*, x 2; B. *L. lesueuri*, x 2; C. *L. eucnemis*, x 5; D. *Nyctimystes zwiefeli*, x 2; E. *Adelotus brevis*, x 5; F. *Assa durlingtoni*, x 5; G. *Crinia georgiana*, x 5; H. *Cyclorana novae-hollandiae*, x 2; I. *Geocrinia laevis*, x 5; J. *Glauertia orientalis*, x 5; K. *Heleioporus albopunctatus*, x 2; L. *Kyarranus* sp., x 5; M. *Lechriodus fletcheri*, x 5; N. *Limnodynastes peroni*, x 5; O. *Mixophyes fasciolatus*, x 2.

POST-MORTEM CHANGES

Disintegration of the pelvic girdle into its component bones has been observed in species in which cartilage is most extensive. Species that are heavily ossified remain intact.

During the process of dehydration, the acetabular fossa may become distorted and, in the material available, such distortion takes the form of compression in a dorsoventral direction. The dorsal crest of the ilium is par-

TABLE 1  
 Characteristics of the Ilium in species of *Litoria*

Species	Profile of ventral acetabular expansion	Dorsal prominence/ anterior rim of Acetabulum	Acetabular rim/ventral ilial shaft margin	Pubis	Position of medial rim on Ilium
<i>adelaidensis</i>	concave	level	above	cart.	ant. $\frac{1}{2}$
<i>angiana</i> *	concavo-convex	posterior	level	cart.	absent
<i>aurea</i>	concave	$\frac{1}{2}$ anterior	above	cart.	ant. $\frac{1}{2}$
<i>bicolor</i>	concave	$\frac{1}{2}$ anterior	above	cart.	?absent
<i>booroolangensis</i>	concavo-convex	$\frac{1}{2}$ anterior	level	bony	central $\frac{1}{2}$
<i>brevipalmata</i>	concave	level	above	cart.	ant. $\frac{1}{2}$
<i>caerulea</i>	concave	level	level	cart.	absent
<i>citropa</i>	concave	level	above	cart.	ant. $\frac{1}{2}$
<i>dorsalis</i> *	concavo-convex	$\frac{1}{2}$ anterior	level	cart.	ant. $\frac{1}{2}$
<i>eucnemis</i>	concavo-convex	level	above	bony	ant. $\frac{1}{2}$
<i>ewingi</i>	concave	level	above	cart.	post. $\frac{1}{2}$
<i>gracilentula</i>	concavo-convex	$\frac{1}{2}$ anterior	above	cart.	absent
<i>infrafrenata</i>	concave	$\frac{1}{2}$ anterior	above	cart.	ant. $\frac{1}{2}$
<i>lesueuri</i>	concavo-convex	$\frac{1}{2}$ anterior	level	bony	central $\frac{1}{2}$
<i>microbelos</i>	concavo-convex	level	above	cart.	ant. $\frac{1}{2}$
<i>nannotis</i>	concavo-convex	level	above	bony	absent
<i>nasuta</i>	concavo-convex	$\frac{1}{2}$ anterior	above	cart.	ant. $\frac{1}{2}$
<i>nigrofrenata</i>	concavo-convex	$\frac{1}{2}$ anterior	above	bony	ant. $\frac{1}{2}$
<i>rubella</i>	concave	$\frac{1}{2}$ anterior	above	cart.	?absent
<i>rothi</i>	concave	$\frac{1}{2}$ anterior	above	cart.	absent
<i>thesaurensis</i> *	concavo-convex	level	above	bony	ant. $\frac{1}{2}$

\* Species restricted to New Guinea.

ant.—anterior; cart.—cartilaginous.

ticularly subject to post-mortem distortion, commonly bending medially from a perfectly vertical orientation to form a quadrant. Even more conspicuous is the distortion amongst material recovered from owl pellets where there has been an induced medial curvature of the ilial shaft in several specimens.

#### Account of modern genera and species

##### Family HYLIDAE

##### LITORIA Tschudi

##### FIG. 3A-C

*Species examined:* *L. adelaidensis* (Gray), *L. angiana* (Boulenger), *L. aurea* (Lesson), *L. bicolor* (Gray), *L. booroolangensis* (Moore), *L. brevipalmata* Tyler, Martin & Watson, *L. caerulea* (White), *L. citropa* (Tschudi), *L. dorsalis* Macleay, *L. eucnemis* (Lönnerberg), *L. ewingi* Dumeril & Bibron, *L. gracilentula* (Peters), *L. infrafrenata* (Gunther), *L. lesueuri* Dumeril & Bibron, *L. microbelos* (Cogger), *L. nannotis* (Andersson), *L. nasuta* (Gray), *L. nigrofrenata* (Gunther), *L. rubella* (Gray), *L. rothi* (de Vis), *L. thesaurensis* (Peters).

Variation in this morphologically and ecologically diverse genus renders a generic definition a difficult proposition. For this reason comparative data are included in Table 1, and only the following generalisations are possible:

The pubis is cartilaginous or ossified and the ischium is ossified.

The ilial shaft lacks a dorsal crest but invariably bears a narrow rim on at least a portion of the medial surface. In *L. aurea* there is also a lateral groove exhibiting a distinct ontogenetic trend in becoming progressively less conspicuous. The acetabular fossa tends to be rather large. The ventral acetabular expansion is of a variety of forms, from a narrow, concave profile to concavo-convex.

The dorsal protuberance and dorsal prominence are usually well differentiated but are not raised high above the level of the ilial shaft.

##### NYCTIMYSTES Stejneger

##### FIG. 3D

*Species examined:* *N. tympanocryptis* (Andersson and *N. zweifeli* Tyler of New Guinea.

TABLE 2  
*Generic features of Iliia*

	Iliac shaft crest	Iliac shaft rim	Dorsal protuberance	Dorsal pro- minence/ anterior rim of acetabulum
<i>Adelotus</i>	absent	present	prominent	anterior
<i>Assa</i>	absent	absent	inconspicuous	level
<i>Cophixalus</i>	absent	absent	inconspicuous	anterior
<i>Crinia</i>	absent	present	inconspicuous	anterior
<i>Cyclorana</i>	absent	present or absent	inconspicuous	anterior
<i>Geocrinia</i>	absent	absent	absent	level
<i>Glauertia</i>	absent	absent	inconspicuous	anterior
<i>Heleioporus</i>	absent	absent	prominent	anterior
<i>Kyarranus</i>	absent	present	prominent	anterior
<i>Lechriodus</i>	present	absent	moderate	posterior
<i>Limnodynastes</i>	present or absent	present or absent	prominent	ant. or level
<i>Litoria</i>	absent	present or absent	moderate	usually anterior
<i>Mixophyes</i>	present	absent	inconspicuous	anterior
<i>Myobatrachus</i>	absent	absent	absent	posterior
<i>Neobatrachus</i>	absent	absent	prominent	anterior
<i>Notaden</i>	absent	absent	prominent	posterior
<i>Nyctimystes</i>	absent	absent	moderate	level
<i>Phyllorhina</i>	absent	present	inconspicuous	anterior
<i>Pseudophryne</i>	absent	absent	moderate	level
<i>Rana</i>	present	absent	inconspicuous	posterior
<i>Ranidella</i>	absent	absent	moderate	anterior
<i>Rheobatrachus</i>	absent	absent	prominent	posterior
<i>Sphenophryne</i>	absent	absent	inconspicuous	posterior
<i>Taudactylus</i>	absent	absent	prominent	anterior
<i>Uperoleia</i>	absent	absent	prominent	anterior

The ilium and ischium are ossified in both species. The pubis is ossified in *zweifeli* and cartilaginous in *tympanocryptis*.

The iliac shaft is long, curved distally and very slightly compressed mediolaterally. The ventral acetabular expansion is gently rounded in a single, uninterrupted concave arc. The acetabular fossa is prominent, with its upper margin level with the centre of the iliac shaft. The dorsal prominence and dorsal protuberance are small and project laterally rather than superiorly. The anterior margin of the dorsal protuberance is on a level with the anterior margin of the acetabular rim. The dorsal acetabular expansion is only slightly raised.

Family **LEPTODACTYLIDAE**  
**ADELOTUS** Ogilby  
FIG. 3E

*Species examined:* *A. brevis* (Gunther).

The ischium is bony and the pubis is entirely cartilaginous.

The iliac shaft is distinctly curved and bears a narrow indentation on the medial surface. This indentation is deepest in the midsection of the shaft. The acetabulum has a narrow peripheral rim which superiorly is on a level with or is slightly superior to the ventral surface of the iliac shaft. The ventral acetabular expansion is only slightly developed, and the preacetabular zone is extremely narrow. The dorsal acetabular expansion is elongate and raised moderately. The dorsal prominence is poorly defined. The dorsal protuberance is extremely large, inclined posteroventrally and is almost entirely anterior to the anterior rim of the acetabular fossa.

ASSA Tyler  
FIG. 3F

*Species examined:* *A. darlingtoni* (Loveridge).

The pubis and ischium are bony except for the portion associated with the posterior half of the acetabular fossa.

The ilial shaft is slightly curved, lacks ridges and indentations and is circular in cross section. The acetabulum has an exceptionally well developed peripheral rim which superiorly is very slightly above the ventral margin of the ilial shaft. The ventral acetabular expansion is slightly developed into a narrow preacetabular zone. The dorsal acetabular expansion is very poorly developed. The dorsal prominence is only slightly defined. The dorsal protuberance is small but prominent, its anterior margin on a level with the anterior margin of the acetabular rim.

#### CRINIA Tschudi

##### FIG. 3G

*Species examined:* *C. georgiana* Tschudi.

The pubis is cartilaginous and the ischium is ossified.

The ilial shaft is curved, flattened medio-laterally over the posterior half and dorsoventrally over the anterior half. There is no dorsal ilial crest but there is a very slight longitudinal medial indentation. The acetabulum is large, has a fairly broad peripheral rim which superiorly is very slightly above the level of the ventral margin of the ilial shaft. The ventral acetabular expansion is only slightly developed; the subacetabular zone does not protrude anteriorly. The dorsal acetabular expansion is poorly developed. The dorsal prominence is low, but quite distinguishable from the ilial shaft. The dorsal protuberance is just detectable. Slightly less than one-half of the dorsal protuberance is anterior to the anterior rim of the acetabulum.

#### CYCLORANA Steindachner

##### FIG. 3H

*Species examined:* *C. australis* (Gray), *C. dahl* (Boulenger), *C. novaehollandiae* Steindachner and *C. platycephalus* (Gunther).

The ischium is bony and fused to the ilium, whereas the pubis can be extensively ossified and similarly fused (*C. dahl* and *C. novaehollandiae*), or completely cartilaginous (*C. australis* and *C. platycephalus*).

The ilial shaft is slightly curved and either bears a narrow dorsal rim, rendered conspicuous by a longitudinal indentation on the medial surface of the shaft (*C. australis*, *C. dahl* and *C. novaehollandiae*), or else lacks a dorsal rim (*C. platycephalus*). The acetabulum has a narrow peripheral rim which superiorly is above the level of the ventral surface of the ilial shaft. The ventral acetabular expansion is slightly developed and the preacetabular zone

is narrow. The dorsal acetabular expansion is prominent and conspicuous. The dorsal prominence is distinguishable from the ilial shaft but only slightly raised. The dorsal protuberance is inclined ventrolaterally, extends far from the prominence, and is approximately one-half anterior to the anterior rim of the acetabular fossa.

#### GEOCRINIA Blake

##### FIG. 3I

*Species examined:* *G. laevis* (Gunther).

The pubis is cartilaginous and the ischium is ossified.

The ilial shaft is short, slightly curved and flattened laterally in cross-section. The acetabulum is moderate with a narrow peripheral rim. The superior margin of the acetabulum lies slightly above the level of the ventral margin of the ilial shaft. The ventral acetabular expansion is only slightly dilated. The dorsal acetabular expansion is not pronounced. The dorsal prominence is small and the dorsal protuberance is not detectable as a distinguishable area. The dorsal prominence is on a level with the anterior rim of the acetabulum.

#### GLAUERTIA Loveridge

##### FIG. 3J

*Species examined:* *G. orientalis* Parker.

The pubis and ischium are entirely cartilaginous.

The ilial shaft has an almost horizontal dorsal surface, and a slightly curved ventral one, so creating a slight broadening at the extremities of the shaft. There is neither a rim nor a crest to the shaft. The acetabulum has a scarcely detectable peripheral rim which superiorly is above the level of the ventral surface of the ilial shaft. The ventral acetabular expansion is slightly developed and the preacetabular zone is slender. The dorsal acetabular expansion is poorly developed. The dorsal prominence is difficult to distinguish from the prominent and evenly rounded dorsal protuberance which appears to be inclined laterally. Approximately one half of the length of the dorsal protuberance lies anterior to the anterior rim of the acetabulum.

#### HELEIOPORUS Gray

##### FIG. 3K

*Species examined:* *H. albopunctatus* Gray.

The pubis and ischium are ossified.

The ilial shaft is not curved but has a slightly undulating superior face, raised into a thickened ridge on the posterior half. The

acetabulum is small and is surrounded by an obliquely tapering rim. The acetabulum is high and is bisected by the ventral margin of the ilial shaft. The ventral acetabular expansion is only slightly dilated but the dorsal acetabular expansion rises sharply. The dorsal prominence is vast and the dorsal protuberance simply an elongate, semi-cylindrical ridge. At least two-thirds of the dorsal protuberance lies anterior to the anterior rim of the acetabulum.

**KYARRANUS Moore**

**FIG. 3L**

*Species examined:* *K. sphagnicolus* Moore, *Kyarranus* sp.

The pubis and ischium are almost entirely bony, only the central portion of the acetabular fossa remaining cartilaginous.

The ilial shaft is strongly curved and almost circular in cross section, but for an indistinct and narrow rim on the posterior half. This rim is created by an indentation of the medial surface of the shaft. The ventral acetabular expansion is poorly developed and the preacetabular zone is very narrow. The dorsal acetabular expansion is quite prominent. The dorsal expansion is scarcely distinguishable from the large and oval, posteroventrally inclined dorsal prominence. The anterior margin of the dorsal prominence is considerably anterior to the anterior rim of the acetabulum.

**LECHRIODUS Boulenger**

**FIG. 3M**

*Species examined:* *L. melanopyga* (Doria).

The pubis is cartilaginous and the ischium ossified.

The ilial shaft is slightly curved and bears an enlarged, fanlike dorsal crest arising from the posterior three-quarters of the shaft. The acetabulum is small and has a broad peripheral rim; the dorsal margin lies above the ventral margin of the ilial shaft. The ventral acetabular expansion is only slightly developed. The dorsal acetabular expansion is long and projects posteriorly. The dorsal prominence is small but detectable and the dorsal protuberance can be distinguished. The anterior margin of the dorsal protuberance is slightly posterior to the anterior rim of the acetabulum.

**LIMNODYNASTES Fitzinger**

**FIG. 3N**

*Species examined:* *L. convexiusculus* (Macleay), *L. dumerilli* Peters, *L. ornatus* (Gray), *L. peroni* (Dumeril & Bibron), *L. salmini* Stein-

dachner, *L. spenceri* Parker, *L. tasmaniensis* Gunther, *L. terraereginae* Fry.

The pubis is cartilaginous and the ischium is ossified.

The ilial shaft is slightly curved and highly variable in structure. There is an elongate groove on the medial surface in *L. dumerilli*, a short groove in *L. terraereginae*, a short lateral groove in *L. tasmaniensis*, and there is a distinct dorsal crest in *L. ornatus* and *L. spenceri*. The acetabulum is small and high, bisected in most species by the ventral margin of the ilial shaft. The ventral acetabular expansion is small and not particularly expanded. The dorsal acetabular expansion rises into a moderate or else high and acutely pointed spike. The dorsal prominence is conspicuous in all species except those with crests on the shafts. It tends to form a conical shape in profile, but is somewhat broader and rounded in the largest species. The dorsal protuberance is an elongate ridge or expanded knob upon the tip of the dorsal prominence. The dorsal protuberance is on a level with or slightly anterior to the anterior rim of the acetabulum.

**MIXOPHYES Gunther**

**FIG. 3O**

*Species examined:* *M. fasciolatus* Gunther.

The pubis and ischium are completely ossified.

The ilial shaft is slightly curved and bears an enlarged fan-like dorsal crest arising dorso-laterally from the length of the shaft. The acetabulum has a broad peripheral rim, the dorsal margin of which lies above the ventral margin of the ilial shaft. The ventral acetabular expansion is moderately developed but with a rather narrow preacetabular zone. The dorsal acetabular expansion rises high to abut the enlarged superior portion of the ischium. There is no dorsal prominence, and the dorsal protuberance is entirely laterally directed and so poorly developed that it is detectable only when the area is viewed from the dorsal or ventral aspects. The anterior margin of this weak protuberance is located anterior to the anterior rim of the acetabulum.

**MYOBATRACHUS Schlegel**

**FIG. 4A**

*Species examined:* *M. gouldii* (Gray).

The ischium is a large and almost circular bony plate, and the pubis is reduced to a small, triangular wedge of cartilage.

The ilial shaft is distinctly curved, lacks crests and indentations and is slightly flattened

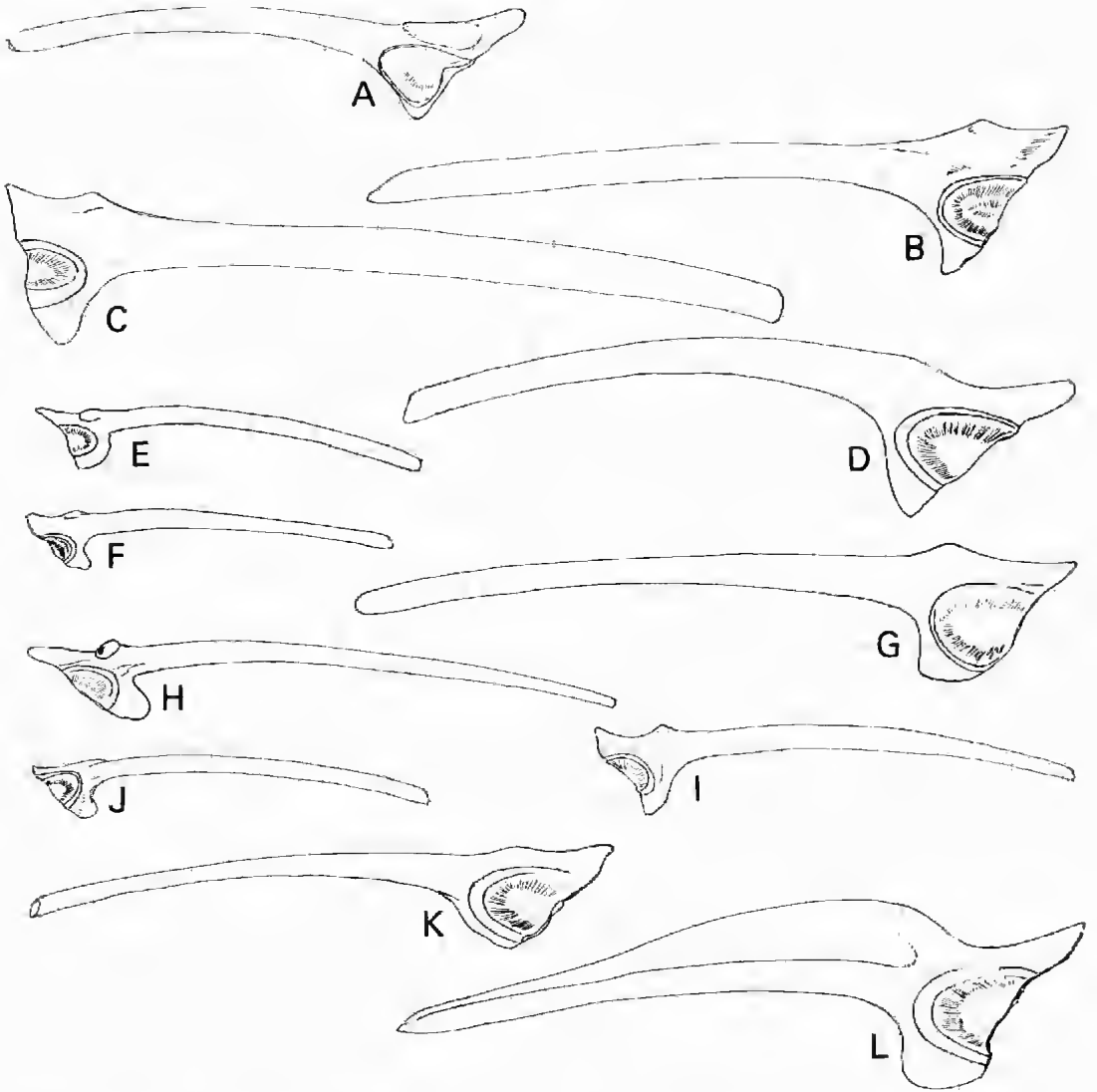


Fig. 4. Pelvis or isolated ilia of leptodactylid, microhylid and ranid frogs:

A. *Myobatrachus gouldii*, x 5; B. *Notaden melanoscaphus*, x 5; C. *Neobatrachus centralis*, x 5; D. *Philoria frosti*, x 5; E. *Pseudophryne bibroni*, x 5; F. *Ranidella parinsignifera*, x 5; G. *Rheobatrachus silus*, x 5; H. *Taudactylus diurnus*, x 5; I. *Uperoleiu* sp., x 5; J. *Cophixalus ornatus*, x 5; K. *Sphenophryne robusta*, x 12.5; L. *Rana papua*, x 5.

laterally, producing an oval cross section. The acetabulum is large and has a narrow peripheral rim whose superior margin is considerably above the level of the ventral surface of the ilial shaft. The ventral acetabular expansion is greatly reduced, consisting of just a slender slip of bone bordering the acetabular rim. The dorsal acetabular expansion is a more prominent feature, rising above the ilial shaft. There is no dorsal prominence, and the dorsal protuberance is replaced by an oval, dorso-

laterally inclined plate, consisting of a weak peripheral rim surrounding a very shallow depression. The anterior margin of this structure is far posterior to the anterior margin of the rim of the acetabular fossa.

#### NEOBATRACHUS Peters

##### FIG. 4C

*Species examined: N. centralis* Parker.

The pubis is cartilaginous and the ischium is ossified.



The ilial shaft is almost perfectly straight. The acetabulum is small and high, the ventral margin of the ilium being on a level with the anterior one-third of the acetabulum. The ventral acetabular expansion is only slightly dilated, the preacetabular zone being particularly reduced. The dorsal acetabular expansion is high. The dorsal prominence is very large and the dorsal protuberance is a pointed nodule upon it. Approximately one-half of the dorsal protuberance lies anterior to the anterior rim of the acetabulum.

**NOTADEN** Gunther

**FIG. 4B**

*Species examined:* *N. melanoscapus* Hosmer.

The pubis and ischium are cartilaginous, the latter with a median calcified zone.

The ilial shaft is only very slightly curved, lacks ridges and indentations and is circular in cross section. The acetabulum has a distinct, flattened peripheral rim which superiorly is on a level with the ventral surface of the ilial shaft. The ventral acetabular expansion is slightly developed with a narrow preacetabular zone. The dorsal acetabular expansion is small and moderately developed. The dorsal prominence is broad and clearly demarcated from the ilial shaft. The dorsal protuberance is small and located on a level above the centre of the acetabular fossa.

**PHILORIA** Spencer

**FIG. 4D**

*Species examined:* *P. frosti* Spencer.

The pubis is cartilaginous and the ischium ossified.

The ilial shaft is strongly curved and has a medially directed dorsal rim. The acetabulum is large, its superior margin on a level with the ventral margin of the ilial shaft. The ventral acetabular expansion is not obviously dilated. The dorsal acetabular expansion is moderately well developed. The dorsal prominence is not conspicuous and the dorsal protuberance scarcely detectable as a separate entity. The dorsal protuberance is almost entirely anterior to the anterior rim of the acetabulum.

**PSEUDOPHRYNE** Fitzinger

**FIG. 4E**

*Species examined:* *P. bibroni* Gunther, *P. coriacea* Keferstein.

The pubis is cartilaginous and the ischium is ossified.

The ilial shaft is almost straight and is circular in cross section. The acetabulum is large

and has a narrow peripheral rim. The superior margin of the acetabulum lies on or slightly above the level of the ventral margin of the ilial shaft. The ventral acetabular expansion is dilated. The dorsal acetabular expansion is only very slightly raised. The dorsal prominence is small (scarcely detectable in *P. coriacea*, but quite distinct in *P. bibroni*) and the dorsal prominence a very small knob on its tip. The dorsal protuberance is on a level with the anterior rim of the acetabulum.

**RANIDELLA** Girard

**FIG. 4F**

*Species examined:* *R. parinsignifera* (Main), *R. signifera* Girard.

The pubis is cartilaginous and the ischium is bony.

The ilial shaft is curved, compressed laterally and possesses neither a rim nor a crest. The acetabulum has a broad peripheral rim which superiorly is on a level with the ventral margin of the ilial shaft. The ventral acetabular expansion is greatly enlarged, the subacetabular zone protruding anteriorly. The dorsal acetabular expansion is poorly developed. The dorsal prominence is broad and the dorsal protuberance is rounded, inclined posteroventrally and moderately prominent. Approximately one-half of the dorsal protuberance is anterior to the anterior rim of the acetabulum.

**RHEOBATRACHUS** Liem

**FIG. 4G**

*Species examined:* *R. silus* Liem.

The pubis is cartilaginous and the ischium ossified.

The ilial shaft is exceptionally slender, very slightly curved and cylindrical in cross section. The acetabulum is very large with a conspicuous rim, its superior margin slightly above the level of the ventral surface of the ilial shaft. The ventral acetabular expansion is slightly dilated. The dorsal acetabular expansion is slightly developed, projecting posteriorly. The dorsal prominence is well developed and the dorsal protuberance is conical and situated posterior to the anterior rim of the acetabulum.

**TAUDACTYLUS** Straughan & Lee

**FIG. 4H**

*Species examined:* *T. diurnus* Straughan & Lee.

The pubis is cartilaginous and the ischium is ossified.

The ilial shaft is gently curved, slightly compressed laterally and possesses neither a rim

nor a dorsal crest. The acetabulum is large with a well developed rim creating a deep acetabular fossa. The ventral acetabular expansion is slightly dilated. The dorsal acetabular expansion is directed posteriorly and overlies the superior margin of the ischium. The dorsal prominence is only slightly distinguishable from the large, raised, oval, dorsolaterally directed dorsal protuberance. Approximately one-half of the dorsal protuberance lies anterior to the acetabular rim.

**UPEROLEIA** Gray

**FIG. 4I**

*Species examined:* *U. marmorata* Gray, *Uperoleia* sp.

The pubis and ischium are cartilaginous.

The ilial shaft is almost straight and is circular in cross section, lacking a rim and a crest. The acetabulum is large and has a broad peripheral rim. The superior margin of the acetabulum lies above the ventral margin of the ilial shaft. The ventral acetabular expansion is of moderate width with the subacetabular zone very slightly expanded. The dorsal acetabular expansion is not pronounced. The dorsal prominence is large and the dorsal protuberance conical and rising far above the level of the shaft. The anterior margin of the dorsal protuberance is situated anterior to the anterior rim of the acetabulum.

**Family MICROHYLIDAE**

**COPHIXALUS** Boettger

**FIG. 4J**

*Species examined:* *C. ornatus* (Fry).

The ischium is small but ossified, and the pubis is cartilaginous.

The ilial shaft is compressed mediolaterally, has neither a rim nor a crest, and is very slightly curved. The ventral acetabular expansion is concave and very narrow. The acetabular fossa is extremely large and very high, its superior margin nearer to the dorsal than the ventral margin of the ilial shaft. The dorsal protuberance is not distinguishable from the dorsal prominence, and lies slightly anterior to the anterior margin of the acetabular rim. The dorsal acetabular expansion is very poorly developed.

**SPHENOPHYNE** Peters & Doria

**FIG. 4K**

*Species examined:* *S. robusta* (Fry).

The ischium is extremely small and only partly ossified. The pubis is cartilaginous.

The ilial shaft is compressed mediolaterally, has neither a rim nor a crest, and is very slightly curved. The ventral acetabular expansion is slightly concave and very narrow. The acetabular fossa is large and high, and is partly bisected by the ventral border of the ilial shaft. The dorsal protuberance is not distinguishable from the dorsal prominence, and lies entirely posterior to the anterior margin of the acetabular rim. The dorsal acetabular expansion is only slightly developed.

**Family RANIDAE**

**RANA** Linné

**FIG. 4L**

*Species examined:* *R. papua* Lesson.

The pubis is cartilaginous and the ischium is bony.

The ilial shaft curves gently downwards and bears a massive fin-like and tapering dorsal crest. The acetabulum is large and bears a broad peripheral rim. The superior margin of the acetabular rim extends considerably above the ventral margin of the ilial shaft. The ventral acetabular expansion has a reduced preacetabular zone and greatly dilated subacetabular zone. The dorsal acetabular expansion is well developed, tapering to a point posteriorly. There is no dorsal prominence and the dorsal protuberance is an oval and almost vertical expansion of the base of the ilial shaft. This protuberance lies entirely posterior to the anterior rim of the acetabulum.

**Fossil genus**

**AUSTRALOBATRACHUS** new genus

*Type species:* *Australobatrachus illus* new species.

This taxon was first reported on by Tyler (1974, p. 711, fig. 1).

Extending from the acetabular region the ilial shaft bears a deep, curved groove on its lateral surface. The acetabular fossa is exceptionally high in relation to the ilial shaft, its superior border reaching a position equivalent to midway up the shaft. The acetabular rim is poorly developed. The dorsal protuberance is gently rounded, and not distinguishable from the dorsal prominence. The anterior limit of the dorsal protuberance is on a level with the anterior margin of the acetabular rim. The ventral acetabular expansion is neither protuberant nor concave, the ilial/preacetabular zone forming almost a straight line extending gradually posteriorly. The dorsal acetabular expansion probably does not project superiorly.

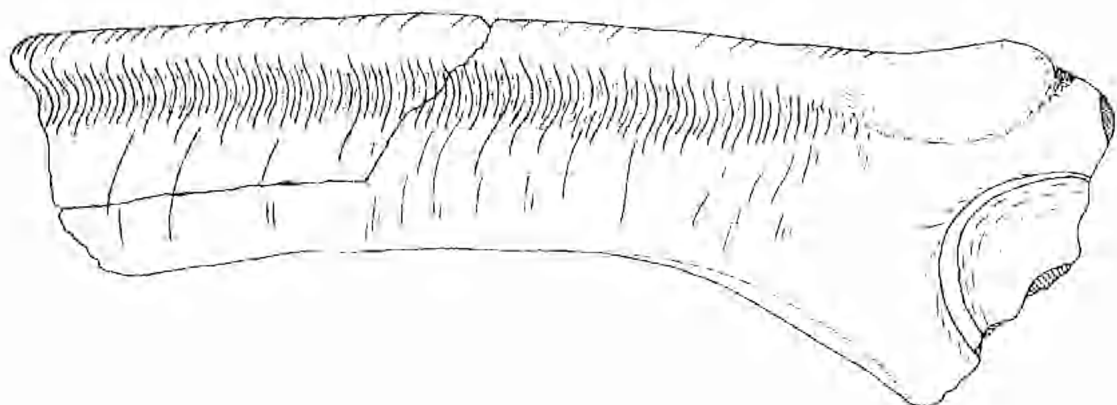


Fig. 5. Left ilium of *Australobatrachus illus* holotype, SAM, P18021.

***Australobatrachus illus* new species**

*Holotype*: Two fragments comprising the distal 6.7 mm of a single left ilium. SAM, P18021 (Fig. 5).

*Type locality*: Tedford Quarry, on the west side of Lake Palankarrina, S.A. (University of California Museum of Palaeontology locality V-5375.)

*Horizon*: Etadonna Formation.

*Age*: Ngapakaldi Fauna, Tertiary; probably mid-Miocene.

*Description of holotype*: As for genus.

*Comparison with other species*: Of the existing families of frogs that do not have modern representatives in Australia, the Leiopelmatidae, Pipidae and Pelobatidae have members in the southern hemisphere and could all be regarded as potential contributors to the ancestral Australian frog fauna; hence their merit comparison with *Australobatrachus*.

The Leiopelmatidae of New Zealand have simple ilia with a slender, cylindrical ilial shaft and a poorly developed ventral acetabular expansion (Stephenson 1960). There is not the slightest resemblance to *Australobatrachus*.

According to Trueb (1973), the pipids are quite unique in possessing a lateral crest (not groove) to the ilial shaft. Any resemblance to *Australobatrachus* has to be weighed against the condition of the dorsal prominence (vast and projecting high above the shaft in pipids; reduced and not raised above the shaft in *Australobatrachus*) and of the ventral acetabular expansion (vestigial in pipids as opposed to being highly developed).

To judge from the descriptions and illustrations of Zweifel (1956) and Kluge (1966) the pelobatid ilium has typically a bow-like dorsal curvature, creating a totally different form from that of *Australobatrachus*. In addition the species illustrated by them have poorly-developed ventral acetabular expansions and more prominent acetabular fossae than has the new genus.

In comparison with the ranids of Australia and New Guinea, *Australobatrachus* is readily distinguished by its total lack of the dorsal crest which rises high above the ranid ilial shaft. Similarly many microhylids (and also some leptodactylids) exhibit such a crest, but the microhylids lacking a dorsal crest may be distinguished by the poor development of the ventral acetabular expansion.

Establishing means of distinguishing Australian hylids from leptodactylids has proved difficult. In general it would appear that a well-developed, dorsally-projecting dorsal prominence is almost characteristic of the leptodactylids, whereas it tends to be poorly developed or else laterally disposed in hylids. Most of the leptodactylids which are exceptional in having poorly-developed dorsal prominences, are those in which the upper section of the ilial shaft is modified in some way. Hence the prominence is scarcely differentiated in *Lechriodus* and *Mixophyes* which have a dorsal crest because the prominence is upon this thin flange of bone. It could be argued that the poor development of the dorsal prominence in *Australobatrachus* conflicts with my interpretation of the groove as an intrinsic modification of the ilial shaft. Hence an alter-

native hypothesis is that the upper rim is the supra-iliac structure, comparable to a dorsal crest. This latter explanation is not favoured, simply because the end section of the ilial shaft is 8-shaped, and the nature of the acetabulum (a poorly developed rim) is not usually developed on a pelvic girdle in which the acetabulum reaches the upper segment of the shaft.

Amongst the Australian hylids and leptodactylids there is considerable variation in the shape of the ventral acetabular expansion. *Cyclorana australis* and several species of *Litoria* approach the condition displayed by *Australobatrachus*, but in each the dorsal prominence is more highly developed and the lateral groove is lacking.

If *Australobatrachus* lacked a lateral groove the nature of the dorsal prominence and the ventral acetabular expansion would cause me to favour referring the genus to the Hylidae. Hence to avoid over-interpreting the presence

and form of the lateral groove, *Australobatrachus* is assigned tentatively to this family.

*Extrapolation of musculature:* The lateral surface of the ilial shaft is the site of origin of the *musculus iliacus externus*. Any extreme broadening of the lateral surface of the ilial shaft increases the surface area available to this muscle. Unquestionably these are modifications most common in aquatic frogs or species inhabiting streamside situations, members of such genera as *Xenopus*, *Rana*, *Lechriodus* and *Mixophyes*. Certainly it is tempting to attribute a similar functional association for *Australobatrachus*, and hence assume that this animal lived close to permanent water.

#### Acknowledgments

I am deeply indebted to Dr M. O. Woodburne for the opportunity to examine and describe the new fossil genus. Dr J. Ling and Mr N. Pledge read and provided constructive criticisms of the manuscript. Mrs L. Kingston very kindly typed the manuscript.

#### References

- CHANCELL, C. J. (1964).—Some Mio-Pliocene hylids from the Valentine formation of Nebraska. *Amer. Midl. Nat.* **72**, 211-225.
- HOLMAN, J. A. (1965).—Early Miocene anurans from Florida. *Quart. J. Florida Acad. Sci.* **28**, 68-82.
- KLUGE, A. G. (1966).—A new pelobatid frog from the Lower Miocene of South Dakota with a discussion of the evolution of the *Scaphiopus-Spea* complex. *Contrib. Sci. Los Angeles County Mus.* (113), 1-26.
- LYNCH, J. D. (1963).—Additional evidence for the recognition of *Limnaeodus* (Amphibia: Hylidae). *Copeia* 1963, 566-568.
- LYNCH, J. D. (1971).—Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. *Misc. Publ. Univ. Kansas Mus. Nat. Hist.* (53), 1-238.
- STEPHENSON, E. M. (1960).—The skeletal characters of *Leiopelma hamiltoni* McCulloch, with particular reference to the effects of heterochrony on the genus. *Trans. R. Soc. N.Z.* **88**(3), 473-488.
- TRUEB, L. (1973).—Bones, frogs and evolution. In Vial, J. (Ed.), "Evolutionary Biology of the Anurans. Contemporary Research on Major Problems", pp. 65-132. (Univ. Missouri Press.)
- TYLER, M. J. (1974).—First frog fossils from Australia. *Nature* **248**(5450), 711-712.
- ZWEIFEL, R. G. (1956).—Two new pelobatid frogs from the Tertiary of North America and their relationships to fossil and recent forms. *Am. Mus. Novit.* (1762), 1-45.